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ON THE REPRODUCTIVE CYCLE AND BREEDING HABITS OF TWO WESTERN SPECIES OF HALIOTIS [1, 2]

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The genus *Haliotis* (Linnaeus) is composed of some 75 species distributed throughout the world. Members of this genus occur from subarctic to antarctic waters, but they are most abundant in temperate and tropical waters as common inhabitants of rocky intertidal and subtidal zones. Because these animals have been of commercial value since ancient times much has been written about their natural history, beginning with Aristotle (see Crofts, 1929). Chance observation of spawning and sporadic examination of the condition of gonads have been recorded by many investigators and fisheries biologists. However, no systematic investigation has been made of the reproductive cycle and breeding habits of haliotids, except for the recent study of gametogenesis in *H. lamellosa* from the Mediterranean Sea (Bolognari, 1954).

In the present study, changes in the size of *Haliotis cracherodii* and *H. rufescens* gonads relative to body size were followed throughout the year.

Materials and Methods

H. cracherodii and *H. rufescens* were collected at Hopkins Marine Station, Pacific Grove, California. In this area *H. cracherodii* is found attached to surfaces of overhanging rocks and crevices in the intertidal zone 3 (Ricketts and Calvin, 1948). *H. rufescens* commonly occurs attached to rocky surfaces, from the lowest tide mark down to a depth of approximately 30 feet. Specimens were therefore collected by diving with the aid of self-contained underwater breathing apparatus (SCUBA).

Ten animals of each species were collected monthly and brought to the labora-

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tory for analysis. Measurements of the shell and soft body parts characterizing the population investigated are summarized in Table I. Of 130 *H. cracherodii* collected, 54 were females and 76 males, and of 140 *H. rufescens,* 79 were females and 61 males. These samples, however, are too small to establish a significant difference in the frequency of the sexes.

The gonad—yellow cream-colored in males, and green in females—occurs as a sheath covering a curved, horn-shaped structure, generally referred to as the conical appendage. The center of the cone is occupied by the brown-colored hepatic tissue. This appendage runs along the right side of the shell muscle. In order to expose the conical appendage, the shell was separated from the rest of the animal by a large spatula. The conical appendage, severed near the stomach and immediately frozen in a Deep Freeze at −25° C., was cross-sectioned with a sharp knife at 2.5-cm. intervals from the apex (Fig. 1).

The perimeters of the gonad and hepatic tissues were traced directly on transparent thin plastic of uniform weight. These tracings were cut from the sheet and weighed. The areas of the tissues at the specific cross-sections were finally determined from a standard curve which related the area of the mentioned plastic to its weight.

The size of the gonad and hepatic tissues varies with variations in size of the animals. In order to observe seasonal changes in the quantity of these tissues, the variation related to size *per se* must be taken into account. The index chosen for this purpose is the ratio of the area of the gonad (or hepatic tissue), at any given cross-section of the cone, to the shell length, multiplied by a hundred.

H. cracherodii

The monthly mean values of gonad and hepatic indices, determined from the cross-section of the conical appendage 5 cm. from the apex, are plotted in Figures 2 and 3, respectively. The 95% confidence limits are also plotted for each point. In Figure 4, the hepatic index is superimposed on the gonad index.

These figures show that *H. cracherodii* exhibits an annual reproductive cycle. The gonads enter a period of growth beginning in March, attaining maximum size towards the end of May. Spawning begins in June and continues to October for most members of the population. From November to March the gonads enter a quiescent period and a minimum size is reached. The size of the hepatic gland

TABLE I

Measurements of shell and soft body parts of H. cracherodii and H. rufescens used in the determinations reported

Measurement	*H. cracherodii*		*H. rufescens*	
	Mean	Range	Mean	Range
Total wet weight in g.	587.2	240.0–1020.0	1410.6	622.0–2330.0
Soft body weight in g.	334.6	120.0–581.1	844.7	380.0–1370.0
Shell weight in g.	252.4	80.7–428.0	565.9	194.1–864.5
Shell length in cm.	14.0	10.8–16.5	19.0	15.0–22.5

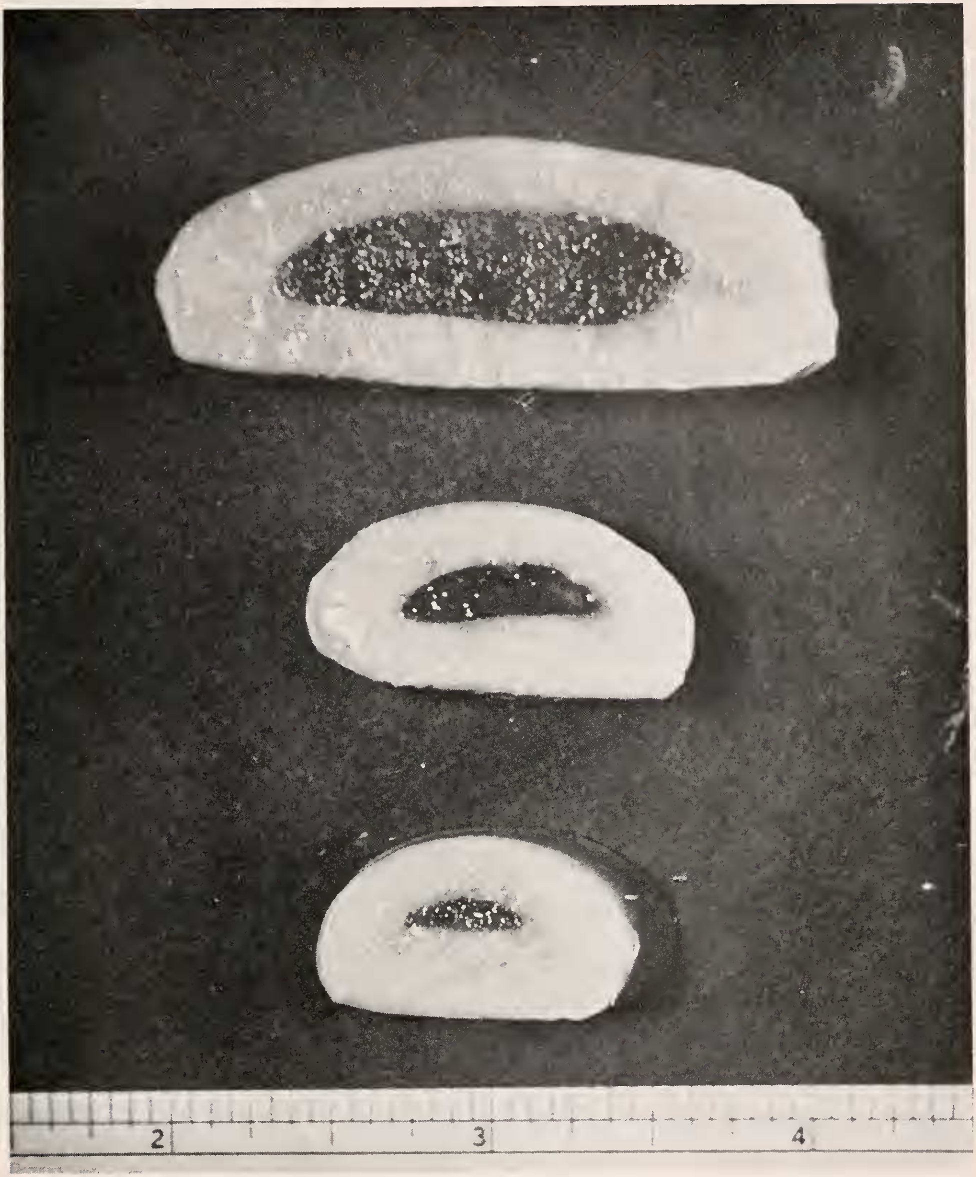

FIGURE 1. Cross-sections of the conical appendage of *H. rufescens*. The dark central region is the hepatic tissue and the light periphery is the gonad tissue. Scale in mm.

exhibits a distinct inverse relation to gonad activity. It undergoes a period of growth beginning in August and reaches its maximum by February. This period corresponds to gonadal quiescence. From February to April there is a precipitous drop in the size of the hepatic gland and this corresponds to the growth period of the gonad. Finally the hepatic index attains a minimum value between April and

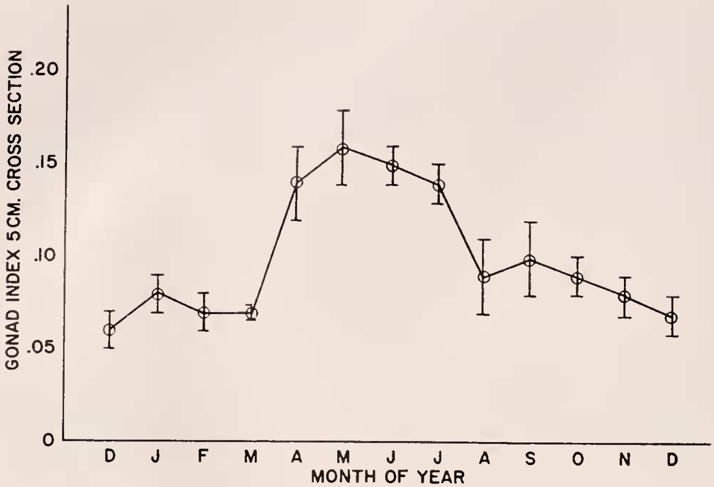

FIGURE 2. Gonad index of the abalone, *H. cracherodii,* for the period December, 1956 to December, 1957. The circles are the mean values and the vertical lines are the 95% confidence limits.

August, during which the gonads are at the height of their activity. These curves suggest that materials are mobilized from the hepatic gland for the growth of the gonad.

Examination of gametes throughout the year showed active sperm and ripe eggs from June to October. Ripe gametes obtained by gonadal biopsies, however, could not be fertilized.

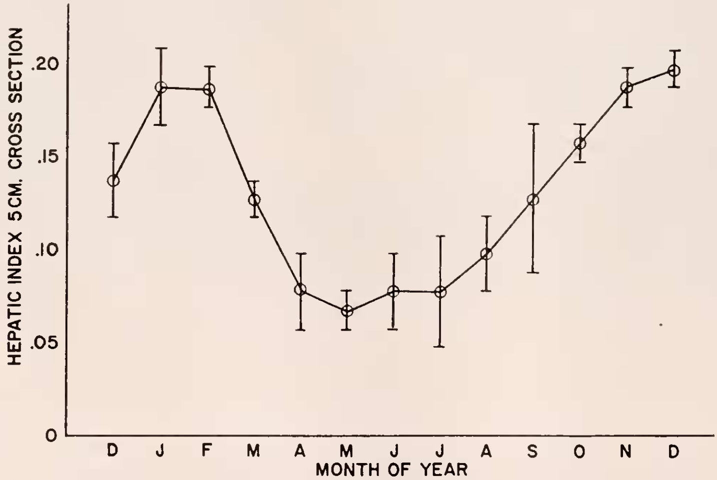

FIGURE 3. Hepatic index of the abalone, *H. cracherodii* for the period December, 1956 to December, 1957. The circles are the mean values and the vertical lines are the 95% confidence limits.

It is of interest to point out that similar results were recently obtained for *H. cracherodii* at Point Dume, in Southern California (Leighton and Boolootian, to be published). This is not only a confirmation of the above observation but also indicates that the cycle observed at Pacific Grove is not restricted to this latitude.

H. rufescens

The monthly mean gonad and hepatic indices of *H. rufescens* are presented in Figures 5 and 6. These figures also show the 95% confidence limits of the mean. Figure 7 presents the hepatic and gonad indices together.

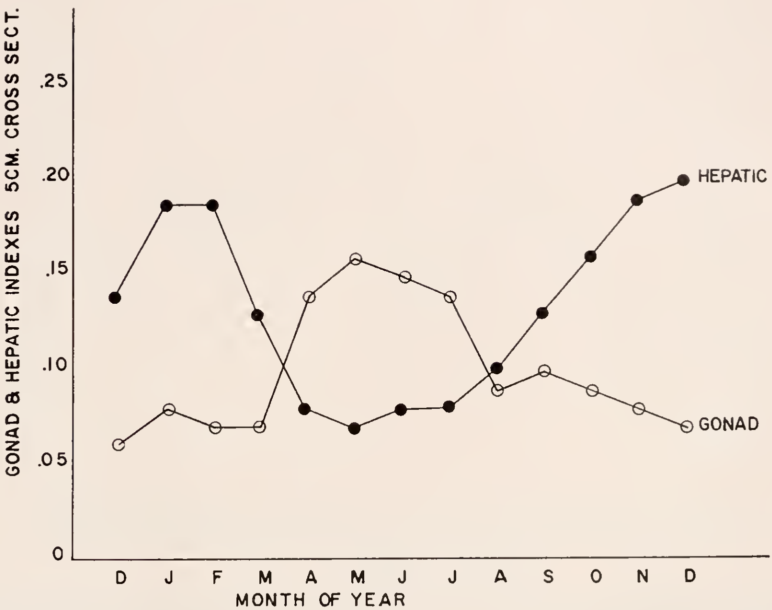

FIGURE 4. The annual gonad and hepatic cycles for *H. cracherodii*. Note inverse relationship between the gonad and hepatic cycles.

In contrast to *H. cracherodii* this organism does not exhibit a distinct reproductive cycle; high gonad and hepatic indices are maintained throughout the year. Monthly examination of the gonad tissues showed ripe gametes at all times, although it was not possible to fertilize the eggs. The inverse relation between gonad size and hepatic indices also holds for this species.

On the basis of the data at hand it is not possible to state whether the fluctuations observed in gonad and hepatic indices represent true seasonal fluctuations. The above data indicate that *H. rufescens*, when considered as a population, breeds throughout the year. This view is further strengthened by evidence presented in Table II, which shows that recently metamorphosed individuals have been recovered from kelp holdfasts throughout most months of the year (Leighton, personal communication).

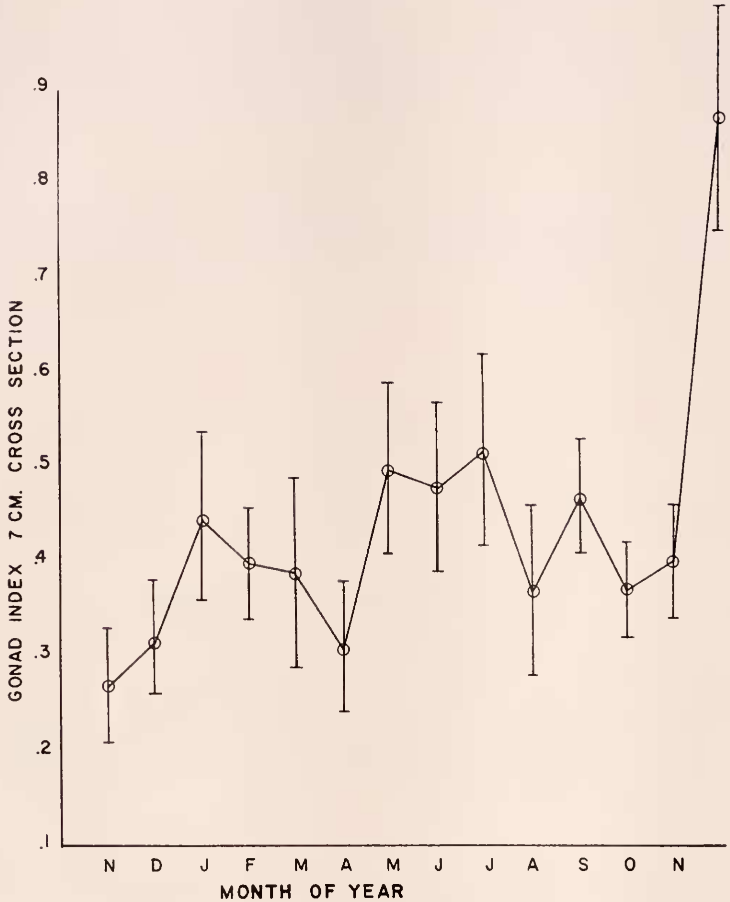

FIGURE 5. Gonad index of the abalone *H. rufescens* for the period November, 1956 to November, 1957. The circles are the mean values and the vertical lines are the 95% confidence limits.

DISCUSSION

Table III is a graphic summary of the breeding seasons reported in the literature for eight species of *Haliotis*, from various parts of the world. Various lengths of breeding season have been reported for *H. rufescens* (Bonnot, 1930, 1940, 1948; Scofield, 1930; Croker, 1931) probably because systematic observations were not made throughout the year. As information was accumulated, the spawning period was extended, and Bonnot (1948) reported it to be from March to September.

Monthly examination of the gonads of this organism at Pacific Grove, California, disclosed mature gametes throughout the year. Furthermore, recently metamorphosed individuals have been found at all seasons in Southern California. It thus appears likely that in both localities *H. rufescens*, considered as a population, breeds throughout the year.

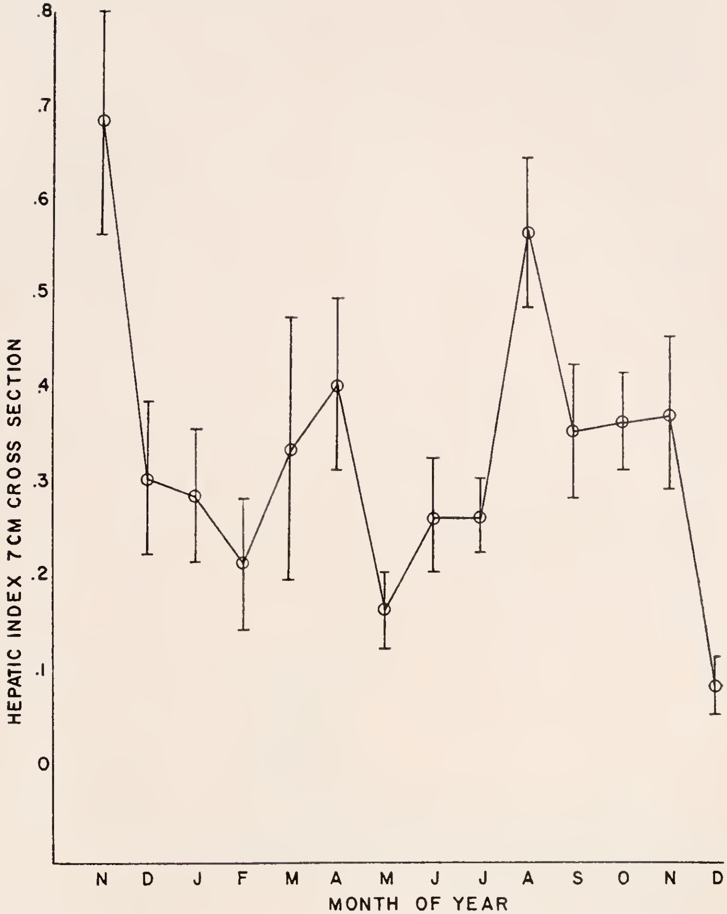

FIGURE 6. Hepatic index of the abalone, *H. rufescens* for the period November, 1956 to November, 1957. The circles are the mean values and the vertical lines are the 95% confidence limits.

The other haliotids seem to have a restricted breeding season. Systematic observation of the reproductive condition of *H. lamellosa* (Bolognari, 1954) at Messina in the Mediterranean Sea indicates that maturation of gametes takes place during March and April. By June the gonads of most individuals attain full maturity and spawning begins. Spawning terminates in October, at which time the gonads enter a quiescent period. *H. cracherodii* at Pacific Grove, California, similarly has a gametogenic period during March and April, the gonads being fully ripe by May and June in most members of a sample. Spawning begins in June and the gonads enter a quiescent period by October. It is interesting to point out that although *H. lamellosa* and *H. cracherodii* occur in widely separated areas, they occur at approximately the same latitude.

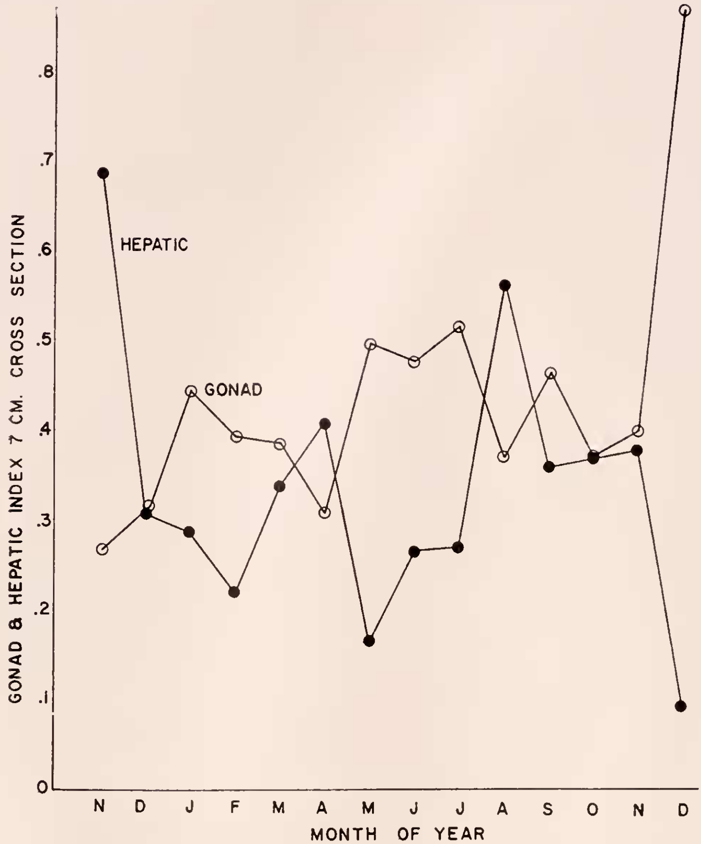

FIGURE 7. The annual gonad and hepatic cycles for *H. rufescens*. Note inverse relationship between the gonad and hepatic cycles, similar to that found for *H. cracherodii*.

Spawning of *H. tuberculata* in the English Channel (Wegmann, 1884; Crofts, 1929, 1937) occurs between May and September much as in *H. cracherodii* and *H. lamellosa*.

Of the four Japanese haliotids presented in Table III, *H. kamtschatkana* is a cold-water species found in Hokkaido. This organism has been observed to spawn from July through November. The other species, *H. gigantea*, *H. sieboldii*, and *H. discus*, are warm-water species occurring further south and are known to spawn later in the season (from October to December). In this group *H. kamtschatkana* has a spawning pattern similar to that of *H. cracherodii*.

The only report of breeding habits for the haliotids of the southern hemisphere is that of Graham (1941) for *H. iris* from New Zealand. He observed a single specimen to spawn in a laboratory aquarium in mid-December. Since December marks the beginning of the summer in the southern hemisphere, this period is seasonally comparable to the spawning period of *H. cracherodii*.

To summarize, with the exception of *H. rufescens*, which apparently spawns

TABLE II

*Recovery of H. rufescens from kelp holdfasts, Macrocystis pyrifera**

Date	Size Range in mm.	Number
9-22-59	2.8–10.0	4
10-24-59	5.0–18.0	4
2-13-60	2.8–8.0	12
4-12-60	3.0–9.3	13
7-18-60	3.0–5.0	3
9-25-60	2.0–25.0	23
10-5-60	1.8–19.0	26
10-18-60	3.0–23.0	16
11-28-60	3.0–8.5	10
12-19-60	3.2–19.0	53
2-6-61	1.0–15.5	33

* All samples were collected from near Scripps Institution of Oceanography, La Jolla, California. Most specimens were found among the sporophytic fronds (Leighton, personal communication).

throughout the year, all the species of *Haliotis* listed above have a spawning period ranging from late spring to early autumn with slight modifications due to local conditions. These may therefore be considered summer breeders.

TABLE III Summary of breeding season of *Haliotis*

The breeding habits of molluscs in general fall into three large categories, namely: (1) year-around breeders, (2) winter breeders which spawn between the end of autumn and the beginning of spring, and (3) summer breeders which spawn between the end of spring and the beginning of autumn. Costello *et al.* (1957) list the breeding season of 24 species of Atlantic molluscs of which 23 breed during the summer and one breeds throughout the year. For the Pacific Coast, MacGinitie and MacGinitie (1949) list 18 species of molluscs; 9 are summer breeders, 6 are winter breeders and three breed throughout the year. Of the 8 species of *Haliotis* considered in this paper, 7 are summer breeders and one breeds throughout the year. Finally, Graham (1941) lists 22 species of molluscs from the New Zealand region, all of which are summer breeders. It thus appears that 85% of the molluscs considered are summer breeders, irrespective of their geographic distribution.

It is beyond the scope of this paper to consider the variety of exogenous and endogenous factors which may affect production and release of gametes in various organisms (see Giese, 1959). It is not possible at this time to do more than speculate about the factors controlling spawning in the abalone. It may seem surprising that such closely related species as *H. rufescens* and *H. cracherodii*, occurring in the same geographic area, exhibit different breeding habits, the former breeding throughout the year, the latter for only a short season. It is possible that seasonal changes in the availability of food (general or specific) determine the period of gamete production. The intertidal species, *H. cracherodii*, is subjected to great variations in the quantity and quality of algae serving as its food, while *H. rufescens*, being subtidal, is subjected to less seasonal variation of this nature (Leighton and Boolootian, to be published).

A distinct increase in the size of the hepatic gland was observed to precede breeding in *H. cracherodii*. Subsequently, as the gonad increased in size the hepatic gland subsided. This reciprocal relation between the hepatic gland and gonad is similar to that found in *Pisaster ochraceus* (Farmanfarmaian *et al.*, 1958). It appears that the hepatic gland stockpiles nutrients essential to gamete development. Stockpiling may occur at a season when the food supply (quantitatively, qualitatively, or both) is most effective. Decisive data for or against this view are lacking.

In *H. rufescens*, no such cycle has been observed, both hepatic gland and gonad being well developed almost throughout the year. It would thus appear that nutrients required for both hepatic and gonadal growth are always available. Only observations on animals under controlled feeding conditions will enable one to determine whether food or some other factors control breeding in these species.

Summary

1. The annual reproductive cycles were determined for two species of abalone: *Haliotis cracherodii* and *H. rufescens*, all found in Monterey Bay. The method consisted of tracing on transparent thin plastic the perimeter of the gonad and hepatic tissues. The tracings were cut and weighed. The areas of these tissues were determined from a standard curve which related the area of the plastic to its weight. The ratio of the area of the gonad (or hepatic tissue) to the shell length

× 100 yields an index for measuring seasonal changes in the quantity of these tissues.

2. *H. cracherodii* shows a marked summer breeding season, the rapid and precipitous spawn-out being indicated by the decline in the size of the gonad.

3. *H. rufescens* shows an ill-defined breeding season and, from reports, seems to spawn at all times of the year. The gonad size was found to vary little during the year except for an increase in winter.

4. In both species the hepatic index is inversely correlated with the gonad index.

5. A summary of the breeding seasons reported in the literature for eight species of *Haliotis* from various parts of the world is discussed.

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